PALYNOLOGICAL NOTES ON AMERICAN SPECIES OF HELIANTHEMUM (CISTACEAE)

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Heydacker (1963) presented palynological evidence purportedly demonstrating that certain American species of the cistaceous genus *Helianthemum* Mill. *sens. lat.* were actually generically distinct and should be considered instead as members of the New World segregate *Crocanthemum* Spach *sens. str.* Since one of us (Daoud and Wilbur, 1965) recently concluded otherwise in connection with a revision of the North American species, an investigation of the pollen of the twenty species recognized from that area and *H. brasiliense* Lam. from eastern South America was undertaken in an effort to evaluate Heydacker's contention.

Crocanthemum was originally described by Spach (1836) to include those American species which he thought possessed only petaliferous flowers. Those American species which he believed to have both petaliferous and apetalous flowers were assigned to his genus *Heteromeris* while species thought to be characterized by only apetalous flowers comprised his genus *Taeniostema*. These three New World genera were judged to be clearly separable from the Old World genera in that they supposedly possessed the combination of alternate, estipulate leaves and short, erect styles.

Many authors have treated all the American representatives of *Helianthemum sens. lat.* as members of the segregate *Crocanthemum sens. lat.* characterized by the above mentioned alternate, estipulate leaves and short, straight styles. Britton (Ill. Fl. N. U.S. 2: 539-541. 1913), Bicknell (Bull. Torrey Club **40:** 613-616. 1913), Janchen (Österr. Bot. Zeitschr. **71:** 266-270. 1920 and Engler and Prantl's Nat. Pflanzenfam. 2 Aufl. 21: 289-313. 1925) and Barnhart (Small's Man. Se. Fl. 878-880. 1933) have all employed *Crocanthemum* in this broadened concept rather than in

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the original restricted usage for species supposedly characterized by the presence of only petaliferous flowers.

Fernald (Rhodora 43: 609-615. 1941) has presented the most careful appraisal of the generic status of *Crocanthemum* known to us. He concluded that there was no justification for the generic segregation of the American species since the morphological features examined supposedly characterizing the genera prove highly inconstant. Such a failing would also cast doubt upon the naturalness of the same groups treated as subgenera or sections. The generic and infrageneric classification of the Cistaceae is not presently in a satisfactory state and doubtless can only be improved by the acquisition of comparative data from numerous botanical subdisciplines. Cytological data on this family are accumulating from the Mediterranean area and Europe and offers promise of providing another useful guide for supraspecific classification within the Cistaceae when a larger percentage of the species have been examined. Only one count has been reported for the approximately forty-five species of the family found in this hemisphere. It seems likely, judging from the limited data already obtained, that systematically meaningful clues to relationship may be derived from detailed palynological studies but in our opinion reclassification is unwarranted until a much broader survey of the family has been undertaken.

Brizicky (1964), like Fernald, concluded that there was not yet sufficient evidence to support the generic segregation of the American species but noted Heydacker's palynological evidence supposedly favoring the retention of apparently all American species within a special section ["tribu"] of *Helianthemum* except for *H. carolinianum* (Walt.) Michx. and *H. brasiliense* (Lam.) Pers. The supposedly very distinctive pollen of these two species convinced her of the validity of *Crocanthemum's* claim for generic recognition.

Heydacker (1963) studied the pollen of 55 species of the Cistaceae and concluded that the palynological evidence supported the recognition of the following seven genera:

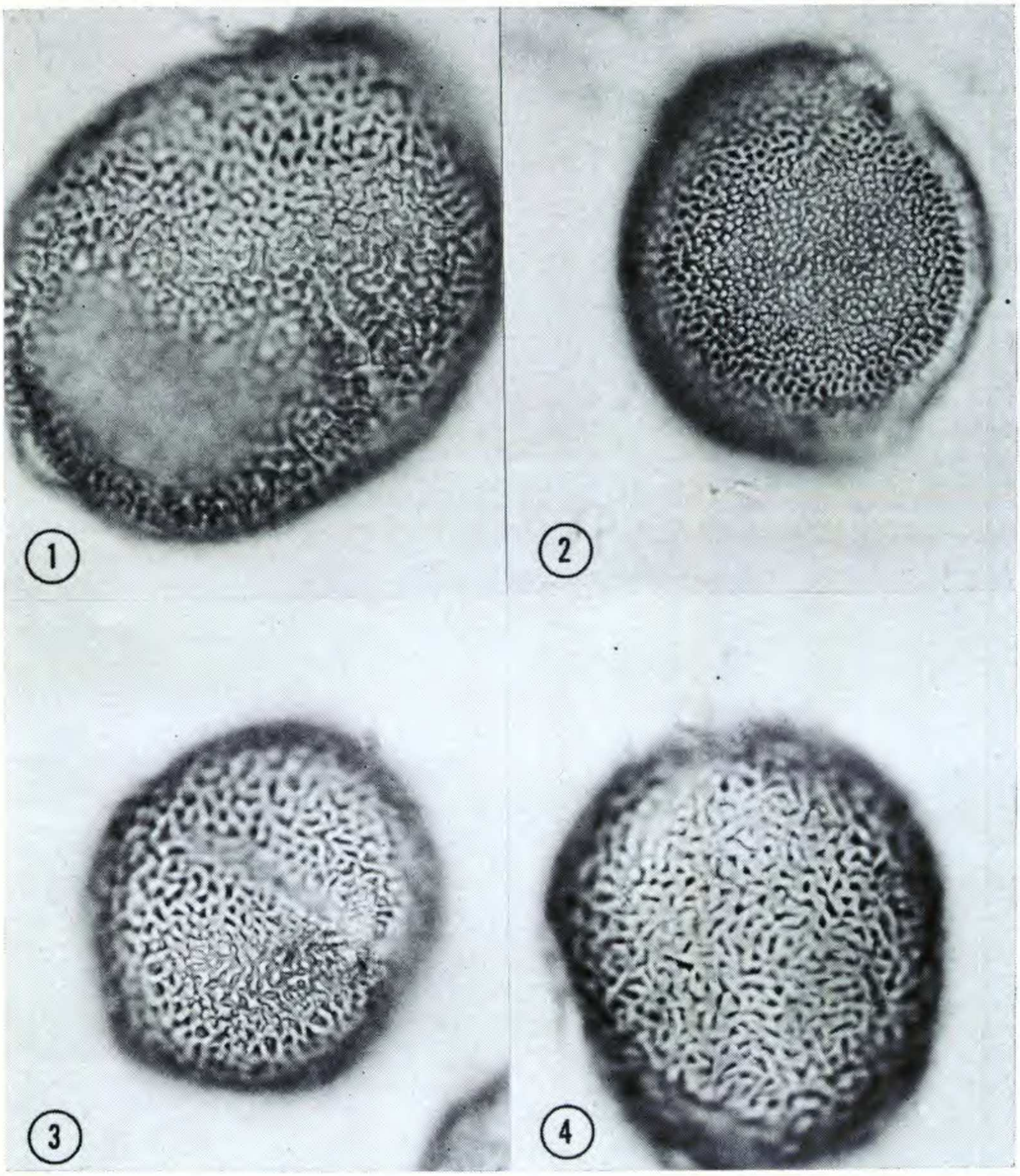
Cistus L., *Crocanthemum* Spach, *Fumana* (Dun.) Spach, *Halimium* (Dun.) Spach, *Helianthemum* Mill., *Hudsonia* L. and *Lechea* L. Unfortunately, Heydacker did not name more than a quarter of the species examined and it is not possible to learn from her account how many species in each genus or how many specimens of each species were examined. Surprisingly enough, Heydacker concluded from palynological evidence that the small Old World genus *Tuberaria*, which is often included within *Helianthemum* itself, is not worthy of generic recognition and on the basis of its pollen might better be included within *Cistus* rather than *Helianthemum*. This conclusion is startlingly in contradiction to the evidence provided by the morphology of the flower and fruit. In contrast Jean and Pons (1963) concluded that palynology supported generic status for *Tuberaria* but demonstrated it to be more similar to *Helianthemum* than to *Cistus*.

The pollen of *Helianthemum* was said by Heydacker to be more elongate than that of the other cistaceous genera and also to be the largest in the family (approximately 80 μ long). She found that the American representatives of *Helianthemum* examined did not conform with their European congeners, for grains of the former often were equiaxial or even shorter than wide. The ratio of polar to equatorial measurements (P/E) of the European representatives was reported to be from 1.2-1.6. The exine proved variable but in the pictured example was striate and rather finely ridged at the base of the elevated striations.

The pollen of *Crocanthemum*, of which both *C. brasiliense* (Lam.) Spach and *C. carolinianum* (Walt.) Spach were examined, was said to be very distinctive. She reported the pollen to be subspherical or slightly short-axial with a P/E ratio of about 0.8. The thickened exine was reportedly reticulate with rather thick or enlarged bases to the elevated network.

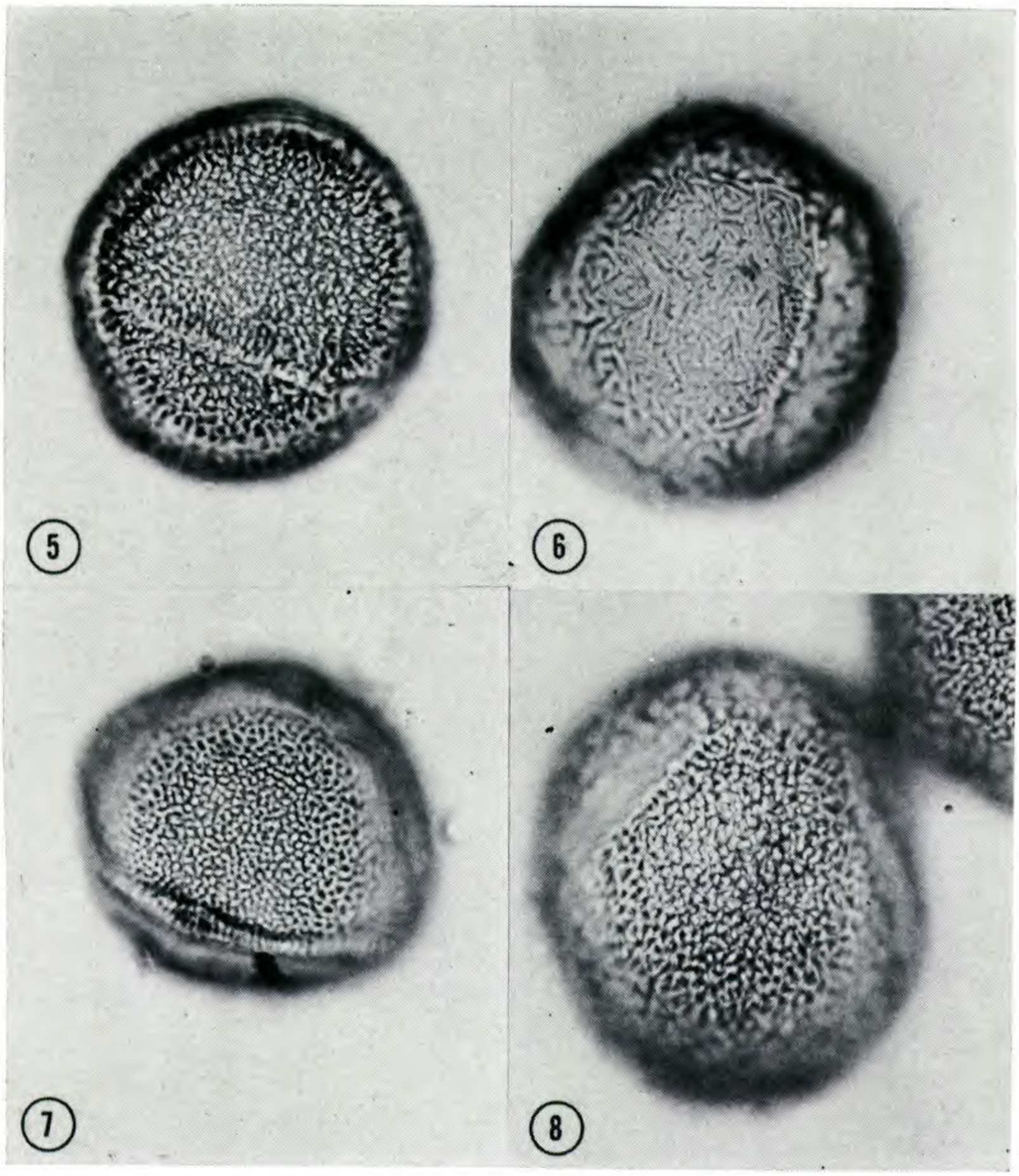
The pollen for our study was prepared for examination by the acetolysis method of Erdtman (1960) from anthers carefully excised from chasmogamous flowers. The prepa-

Plate 1353.



Figs. 1-4. Fig. 1. *Helianthemum brasiliense.*
Fig. 2. *H. corymbosum.* Fig. 3. *H. arenicola.*
Fig. 4. *H. carolinianum.*

Plate 1354.



Figs. 5-8. Fig. 5. *Helianthemum concolor.*
Fig. 6. *H. canadense.* Fig. 7. *H. nutans.*
Fig. 8. *H. greenei.*

ration of the slides was made by Mrs. Shirlee Cavaliere and Mrs. Myra Stewart of Professor D. A. Livingstone's laboratory. We are most appreciative of their assistance. The advice and aid of Dr. Livingstone were most helpful but any mistakes or errors contained in this paper are to be attributed to the authors alone.

A Spencer microscope with 10 X oculars and a 44 X objective was used for measurements which were made to the nearest optical line (1 line = 1.52 μ). Data for Table 1 were obtained by measuring at least 40 fully expanded pollen grains from each collection. In the case of *Helianthemum chihuahuense*, grains allowing a polar diameter measurement were scarce; therefore fewer polar than equatorial diameter measurements were taken. Pollen-wall ornamentations were compared by photographs at 1500 X. Collectors and collection numbers are given in the table.

The information presented in Table 1 in our opinion offers no palynological support for those who contend that the American species are divisible into two or more genera. The ratio of polar/equatorial measurements of *H. carolinianum* and *H. brasiliense* are matched by the P/E ratio of numerous other American species. Variability of the P/E ratio of *H. carolinianum* and *H. brasiliense* was greater than that indicated by Heydacker, ranging from 0.7-1.2 in contrast to the 0.8 reported in her paper. All of the American species studied with a P/E ratio of 0.6-1.2 were lower than or equalled only the lowermost range of that reported for the Old World species of 1.2-1.6. These data, if substantiated with a more meaningful sample, would give only slight additional support to those who have argued that the American species as a group are generically distinct from their Old World relatives. The sculpturing of the exine of *H. brasiliense* and *H. carolinianum* fails also to support the separation of those two species from the remaining American species. Although *H. brasiliense* possessed the coarsest sculpturing of any American species, the sculpturing of *H. carolinianum* was matched by that of several other American species. We cannot confirm Hey-

TABLE 1

SPECIES AND LOCALITY	SCULPTURING	POLAR DIMENSION (μ)			EQUATORIAL DIMENSION (μ)			P/E RATIO
		Mean	St. Dev.	Range	Mean	St. Dev.	Range	
H. arenicola Chapm.: Franklin Co., Fla. Eyles 8270	Coarsely reticulate	45.1	3.6	39.4-51.6	48.4	2.7	44.0-53.1	0.7-1.2
H. argenteum Hemsl.: San Luis Potosi, Mexico. Schaffner 606	Finely reticulate	34.2	1.9	30.4-36.4	37.6	2.8	31.9-42.5	0.7-1.1
H. bicknellii Fern: Webster Mass. Knowlton	Finely reticulate	44.0	2.4	39.4-48.6	50.6	3.1	45.5-57.7	0.7-1.1
H. brasiliense (Lam.) Pers.: Cerro, Departmento de Montevideo, Uruguay. Herter 257	Coarsely reticulate, ridges thickened	50.9	2.5	45.5-54.6	56.6	4.2	51.6-66.8	0.7-1.1
H. canadense (L.) Michx.: Pine Grove, Mass. Gilbert	Elaborately striate	50.0	2.0	45.5-54.6	51.7	2 1	48.6-54.6	0.8-1.1
H. carolinianum (Walt.) Michx.: Screven Co., Ga. Harper 2081	Coarsely reticulate	47.8	3.4	38.0-54.6	51.8	2.9	45.5-57.7	0.7-1.2
H. chihuahuense S. Wats.: Hidalgo, Mexico. Rose 9235	Moderately reticulate	42.5	0.3	41.0-44.0	46.2	3.6	42.5-57.7	0.7-1.0
H. concolor (Riley) Ortega: Coalcoman, Mexico. Hinton 12960	Coarsely reticulate	44.2	1.8	41.0-47.0	46.2	2.0	42.5-50.1	0.8-1.1
H. corymbosum Michx.: Chatham Co., Ga. Harper 2173	Finely reticulate	44.0	1.9	41.0-48.6	48.1	1.9	45.5-51.6	0.8-1.1
H. coulteri S. Wats.: Mexico. Pringle 6672	Finely reticulate	40.2	2.3	36.4-44.0	45.5	2.3	41.0-50.1	0.7-1.1

H. dumosum (Bickn.) Fern.: Barnstable Co., Mass. Woodward & Fernald 15287	Moderately reticulate	45.8	2.2	41.0-48.6	50.1	2.8	45.5-54.6	0.8-1.1
H. georgianum Chapm.: Travis Co., Texas. B. C. Tharp 16041	Moderately reticulate	47.2	1.5	44.0-48.6	49.7	1.5	48.6-51.6	0.9-1.0
H. glomeratum (Lag.) Lag. ex Dunal: Guatemala. Skutch 1119	Moderately reticulate	36.9	2.0	33.4-42.5	38.4	1.6	34.9-41.0	0.8-1.2
H. greenei Robins.: Santa Cruz Island, Calif. Hoffman.	Fine, very densely arranged reticulations	36.9	2.0	33.4-42.5	38.4	1.6	34.9-41.0	0.8-1.2
H. nashii Britt.: Lake Co., Fla. Curtiss 6620	Moderately reticulate	41.8	3.0	39.4-48.6	46.7	2.9	42.5-51.6	0.8-1.1
H. nutans T. S. Brandeg.: Baja California. Moran 10232	Finely reticulate	41.5	2.8	36.4-48.6	48.1	3.0	41.0-53.1	0.7-1.2
H. patens Hemsl.: Jalisco, Mexico. McVaugh 16849	Finely reticulate	39.7	2.3	36.4-42.5	43.3	2.0	39.4-48.6	0.7-1.1
H. pringlei S. Wats.: N.E. Sonora Mexico. White 3513	Finely reticulate	42.1	2.5	39.4-48.6	47.3	2.2	42.5-51.6	0.8-1.1
H. propinguum Bickn.: Nantucket Island, Mass. Bicknell	Moderately reticulate	44.1	2.6	36.4-47.0	48.8	3.8	42.5-56.1	0.6-1.1
H. rosmarinifolium Pursh: Oliver Ga. Curtiss 6838	Finely reticulate	42.5	3.6	36.4-48.6	44.6	2.5	41.0-48.6	0.7-1.2
H. scoparium Nutt.: Del Monte, Calif. Abrams 5208	Moderately reticulate	43.1	1.7	39.4-45.5	47.4	2.5	42.5-51.6	0.8-1.1

dacker's claim that *Crocanthemum* is generically characterized by enlarged bases of the exine columns since those of *H. brasiliense* were indistinctly, if at all, swollen and those of *H. carolinianum* were, in our material, clearly not enlarged basally. Swollen bases to the exine columns of a more pronounced degree were noted in *H. nutans*, *H. greenei* and *H. georgianum*. Electron microscopy, perhaps of the surface scanner type, would doubtless provide more convincing evidence but from what we have observed it would not appear that palynology offers much promise for guidance in the reclassification of the American species of *Helianthemum s.l.* We would conclude therefore that there is no palynological basis yet suggested which would support the separation of *H. brasiliense* and *H. carolinianum* from the other American species or for the maintenance of the generic segregate *Crocanthemum*.

The pollen of the species of *Helianthemum* illustrated by Jean and Pons (1963) in their study of the Cistaceae of France was clearly striate and unlike the reticulate pattern exhibited by all American species examined in this study except *H. canadense*. The pollen of *H. canadense* was also conspicuously striate but unlike the European species illustrated exhibits a very broken surface since the grooves and ridges in one area tend to run in a different direction than those in another. The pollen of *H. canadense* examined by us was by far the most distinctive of the species examined but should doubtless be reinvestigated to determine whether its apparent uniqueness is consistent or an artifact in preparation.

In passing we would like to comment upon Brizicky's (1964) transfer of Grosser's *Halimium* section *Spartioides* to *Helianthemum* apparently with the same circumscription and the same three species as it originally contained. It is not believed that the following statement quoted from Abrams (1951) constitutes valid publication of the transfer of the section from either *Halimium* (Pflanzenreich IV. 193 (Heft 14) 33. 1903) or *Crocanthemum* (Nat. Pflanzenfam. ed. 2. 21: 305. 1925): "The Pacific States species belong

to the section *Spartioides*, characterized by the broom-like habit and the absence of cleistogamous flowers." To attribute this as constituting a new combination by Abrams would be in our opinion contrary to Article 33 of the Code. The two sections of the exclusively American subgenus *Lechioides* (Dunal) Reichenb. were contrasted as follows:

Flowers usually dimorphic; eastern N. and S. America, the West Indies, Mexico, Central America and Chile ..... Sect. *Lechioides*
Flowers homomorphic, broomlike subshrubs; western North America (California and Baja California) and Chile ..... Sect. *Spartioides* (Grosser) Brizicky

This infrageneric classification does not seem satisfactory since there actually are no characters mentioned by Brizicky or known to us which bind the species together. The alleged broomlike habit of the species of Section *Spartioides* actually does not even cover all of the extremely diverse growth forms that are included within *H. scoparium*. Homomorphic species which apparently would be included in section *Lechioides* are the Mexican and non-spartioid *H. nutans* T.S. Brandeg. and *H. patens* Hemsl. Fewer than one per cent of the specimens of *H. carolinianum* (Walt.) Michx. of section *Lechioides* seen had any cleistogamous flowers. It seems to us most unlikely that *H. scoparium* and *H. greenei* will be separated as a group from all the other North American species when enough is known to establish a biologically sound infrageneric classification. In any event the formation of an infrageneric classification might better wait for the discovery of features which bind species into definable groups.

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